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Grazing impacts on Auchenorrhyncha diversity and abundance on a Scottish upland estate

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Abstract. 1. Livestock grazing impacts on insect populations in a variety of ways. For phytophagous insects the impact is primarily a result of altering the structure and species assemblage of vegetation. However not all species react in similar ways and even within an order there may be winners and losers from different grazing regimes.

2. A long-term, replicated, controlled experiment, comprising four grazing treatments, was established within an upland acid grassland area in Scotland. Auchenorrhyncha were sampled by suction sampling and sweep-netting in the fifth year following the start of the treatments.

3. A significant treatment effect was apparent in the suction samples with Auchenorrhyncha abundance being three to four times higher in the ungrazed plots compared to the other treatments. Abundance was also highest from the ungrazed plots in the sweep net samples, but this effect was not statistically significant. Redundancy analysis (RDA) showed that a suite of species which are typical of shaded positions responded with increased abundance in the ungrazed plots.

4. The findings demonstrate that the assemblages found in ungrazed areas can be vastly different to those found in even lightly grazed areas and therefore, underline the benefits of varied grazing regimes in maximising diversity. Furthermore, the work underlines the benefit of employing multiple sampling methods.

Key words. Cattle grazing, grassland, grazing experiment, Hemiptera, insect, leafhopper, plant bug, Scotland, sheep grazing.

Introduction

Much of the open ground in upland Scotland comprises a mosaic of dwarf-shrub-dominated plant communities and semi-natural acid grasslands. The grasslands are extensive (semi-natural acid grassland covers 12.3% of the area of Scotland – Carey *et al*., 2008) and host distinct plant and animal assemblages (e.g. Littlewood *et al*., 2006b). However, they are sometimes viewed by conservation biologists as degraded habitats and thus are often understudied (e.g. Thompson & Brown, 1992).

Grazing by livestock has an important effect on vegetation structure and plant species composition in grasslands (e.g. Olff & Ritchie, 1998) although responses can vary. For example, Kruess and Tscharntke (2002) showed plant species richness to be higher on formerly cattle-grazed pastures where grazing had ceased than on pastures that were currently cattle-grazed whilst, in unimproved mesotrophic pasture, Stewart and Pullin (2008) suggested that grazing at low levels maximised forb species richness. Tallowin *et al*. (2005), on the other hand, found no increase in plant diversity on lowland neutral grassland with a reduction in livestock grazing over a 5 year period.

Although responses of individual species will vary, in general insect abundance, species richness or diversity has been shown to be higher in less-grazed sites with tall vegetation than in more heavily-grazed sites with shorter vegetation (Morris, 2000). This is particulary true of primarily phytophagous taxa (Woodcock *et al*., 2009) with, for example, Lepidoptera (Pöyry *et al*., 2006; Littlewood, 2008) and Auchenorrhyncha (Gibson *et al*., 1992; Fisher Barham & Stewart, 2005) showing clear responses. Assemblages of these and other groups may also be closely linked with plant species composition (e.g. Sanderson *et al*.,

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1995; Littlewood *et al*., 2006a; Schaffers *et al*., 2008). However, there may be discrepancies between the rate of change of plant and insect assemblages (Nickel & Achtziger, 2005; Littlewood *et al*., 2009) and changes in insect diversity may lag behind changes in plant diversity (Southwood *et al*., 1979). Assemblages of grassland Auchenorrhyncha are also sensitive to habitat quality (Hollier *et al*., 2005). They generally are closely related to vegetation with abundance being positively related to sward height and species richness being related to plant species and structural diversity (Hartley *et al*., 2003; Morris *et al*., 2005).

Grasslands are rarely managed specifically for insects and indeed detailed ecological knowledge of the full suite of species present would be impossible to obtain. However, understanding of insect responses to management is a helpful contribution when trying to make informed decisions based on established aims. Hemiptera (of which Auchenorrhyncha form a part) form a significant part of the diet of adult passerine birds (Buchanan *et al*., 2006). Such predators have been shown to structure their foraging based on both abundance and accessibility of prey (Evans *et al*., 2006; Douglas *et al*., 2008; Vandenberghe *et al*., 2009). Information on how insect populations are structured in grasslands is, though, incomplete and there is a need for a wide evidence body on which to base generalised management advice.

Here we look at the impact of different grazing levels on the Auchenorrhyncha assemblage within a long-term experiment at an upland estate in central Scotland. We hypothesise that abundance and species richness will be inversely related to grazing intensity. We further examine which elements of the Auchenorrhyncha assemblage are most impacted by grazing levels in order to be able to provide an ecological interpretation for observed effects.

Methods

Field site

Glen Finglas, Perthshire, Scotland (56°16′N, 4°24′W), is a 4085 ha estate grazed by sheep and cattle. The dominant vegetation in the study areas was acid grassland and mire. The most represented National Vegetation Classification (NVC) communities (Rodwell, 1991, 1992) were M23 (*Juncus effusus/acutiflorus–Galium palustre* rush-pasture), M25 (*Molinia caerulea–Potentilla erecta* mire), U4 (*Festuca ovina–Agrostis capillaris–Galium saxatile* grassland) and U5 (*Nardus stricta–Galium saxatile* grassland). Some areas were covered by bracken (*Pteridium aquilinum*, NVC U20). A small number of isolated trees grew in lower plots, comprising downy birch (*Betula pubescens* Ehrh.); eared willow (*Salix aurita* L.) and rowan (*Sorbus aucuparia* L.), while one block had substantial patches of the shrub bog myrtle (*Myrica gale* L.).

Grazing treatments

A replicated, randomised block experiment was established in 2002 which consisted of 24 enclosures, each measuring 3.3 ha. There were four treatments and these were arranged in six replicate blocks. Altitude and aspect were similar within each replicate block but varied between blocks with an altitudinal range across all plots of 220–500 m. Grazing treatment I was high-intensity sheep grazing at commercial stocking density of 9 sheep per plot (=2.7 sheep ha^{-1}). Treatment II was low-intensity sheep grazing of 3 sheep per plot (=0.9 sheep ha^{-1}); this represented a continuation of the pre-experimental management on the site. Treatment III was low-intensity mixed grazing comprising 2 sheep per plot (=0.6 sheep ha^{-1}) and, for 4 weeks in autumn, two cows each suckling a single calf (=0.6 cows and calves ha^{-1}), giving an equivalent aggregate quantity of livestock units/offtake to treatment II. Treatment IV was ungrazed. Animals were removed from the plots during severe winter weather and for usual farming practices such as dipping against external parasites. The grazing treatments were applied from January 2003.

Sample collection

Sampling was carried out between 1 June and 9 July 2007. Two sampling methods were used: D-vac and sweep-netting. The D-vac (D-vac co., Ventura, CA, USA) takes standard suction samples through a funnel with diameter of 34.3 cm. Samples consisted of five pooled sub-samples of duration 45 s each. Sweep-netting was carried out along a 20 × 0.5 m transect running perpendicular to the slope from the sample point. The sample consisted of approximately 80 sweeps with a net of diameter 45 cm (number of sweeps varied slightly as the transect was standardised by length rather than sweep number). Sampling was carried out in fine dry weather once each at up to five randomly selected locations within each grazing plot. However, poor weather during the sampling period prevented this number from being taken from all plots and, in total, 110 D-vac and 79 sweep net samples were collected.

Auchenorrhyncha were identified using Biedermann and Niedringhaus (2004) and Holzinger *et al*. (2003). Nomenclature follows that used by Biedermann and Niedringhaus (2004). All males were identified to species. Females were identified to species except for those of Delphacidae, which were aggregated as one group, as were the very small numbers of female Aphrodinea and of the genus *Cixius*.

Statistical analysis

Analysis was carried out in Genstat 11.1 (Lawes Agricultural Trust, Hertfordshire, UK). Generalized Linear Mixed Models were used to test for the significance of grazing treatment on abundance and on species richness within both sweep net and D-vac samples. Treatment was present as a fixed effect and grazing plots were nested within blocks which formed the random model. This random model allowed the variation within plots from the different samples to contribute to the analysis whilst keeping the appropriate degrees of freedom for testing the main effects. A Poisson distribution and log-link function was used for the abundance data and a normal distribution was used for species richness data. Significance values were generated by a Wald test.

The proportion of variation in the species data that could be explained by grazing treatment was assessed for each sampling method by carrying out a Redundancy analysis (RDA) within CANOCO 4.5 (ter Braak & Šmilauer, 2002). Samples within each treatment replicate (plot) were averaged to compile the data matrix for analysis and included just those specimens identified to species. A linear RDA model was deemed appropriate due to low species turnover as evidenced by a short axis 1 (<1 for each sampling method) in a Detrended Correspondence Analysis (DCA) of the species data (Lepš & Šmilauer, 2003). Grazing treatment was represented by four binomial environmental variables, which were used to define canonical axes. The significance of all canonical axes together was tested by Monte Carlo Permutation Tests with 999 permutations within blocks defined by the replicate locations.

Results

In total 3319 adult Auchenorrhyncha were recorded comprising 33 species. Of these, 1244 of 21 species were caught by D-vac and 2075 of 31 species were caught by sweep-netting. The species included a range from those that utilise a wide range of habitats through to species that are specialised and rare in the UK at least (for further details, see Littlewood & Stewart, 2011).

Grazing effect on abundance and species richness in D-vac samples

Grazing treatment had a highly significant effect on abundance (Fig. 1) and a significant effect on species richness (Fig. 2) in the D-vac samples (Table 1). The highest median abundance was found in the ungrazed treatment IV (median 24) and the lowest in high-intensity sheep grazing treatment I (median 5). Examination of treatment SE indicated that these two groups were each different from each of the others (means were $>1.96 \times$ SE different to one another, effectively outside their 95% confidence intervals) whilst the intermediate grazing treatments II and III did not differ from each other. For species richness the ungrazed treatment IV differed from all the other treatments which did not differ from each other.

Grazing effect on abundance and species richness in sweep net samples

In the sweep net samples, the highest median abundance was also in the ungrazed treatment IV (median 32) with the lowest in the low-intensity mixed grazing treatment III (median 11.5) though in this case the grazing treatment effect on abundance (Fig. 3) and on species richness (Fig. 4) was not significant (Table 1).

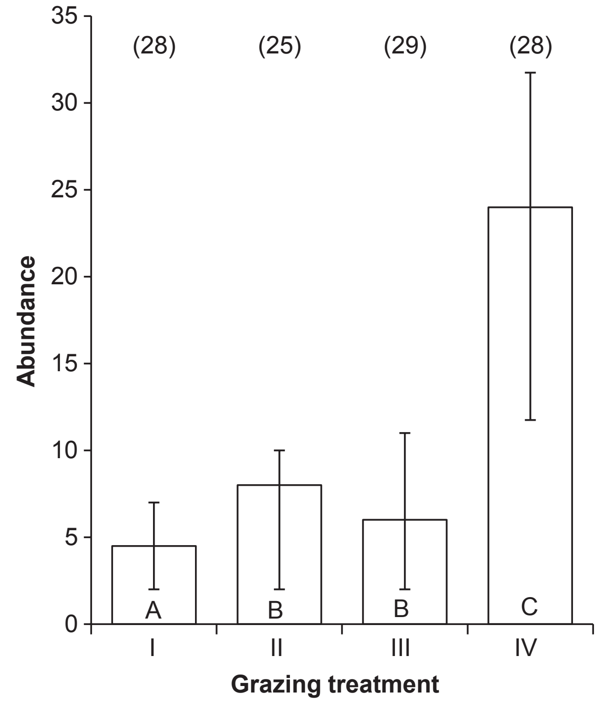

Fig. 1. Median and interquartile range of Auchenorrhyncha abundance in each grazing treatment from D-vac samples. Significantly different groups ($P < 0.05$) are indicated by letters at base of bar. Number of samples is shown in parentheses at the top of the chart. Grazing treatments: I, high-intensity sheep grazing; II, low-intensity sheep grazing; III, low-intensity sheep and cattle grazing; IV, ungrazed.

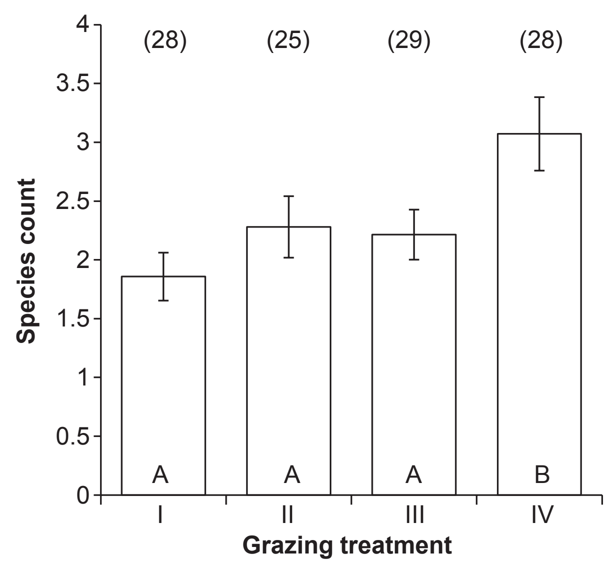

Fig. 2. Mean and SE of Auchenorrhyncha species richness in each grazing treatment from D-vac samples (excludes specimens not identified to species level). Significantly different groups ($P < 0.05$) are indicated by letters at base of bar. Number of samples is shown in parentheses at the top of the chart. Grazing treatments as detailed in Fig. 1.

Table 1. Results of Generalized Linear Mixed Model analysis of grazing treatment effect on Auchenorrhyncha samples collected by D-vac and sweep net showing degrees of freedom.

	n.d.f., d.d.f	Wald/n.d.f	Significance, *P*
D-vac abundance	3, 16.0	12.03	< 0.001
D-vac species richness	3, 13.8	5.34	0.012
Sweep net abundance	3, 13.4	1.53	0.251
Sweep net species richness	3, 9.5	1.08	0.403

n.d.f., numerator degrees of freedom; d.d.f., denominator degrees of freedom.
Wald statistics divided by numerator degrees of freedom and probability values.

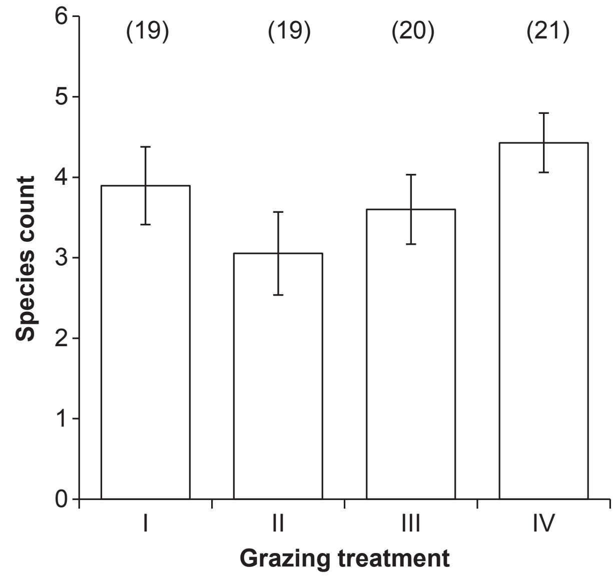

Fig. 4. Mean and SE of Auchenorrhyncha species richness in each grazing treatment from sweep net samples (excludes specimens not identified to species level). Number of samples is shown in parentheses at the top of the chart. Grazing treatments as detailed in Fig. 1.

Grazing effect on assemblage in D-vac samples

The RDA of D-vac samples showed that grazing treatment had a significant effect on the species assemblage data (F = 4.848, P = 0.001). This model explained 42.6% of variation in the assemblage data with a clear separation on axis 1 of the biplot between grazed (I, II and III) and ungrazed (IV) treatments. Sheep grazing treatments (I and II) further separated from the mixed sheep and cattle treatment (III) on axis 2 (Fig. 5). A suite of species were strongly correlated with the ungrazed treatment IV, especially *Javesella discolor*, *J. dubia*, *J. forcipata*, *Paraliburnia clypealis* and *Criomorphus albomarginatus*.

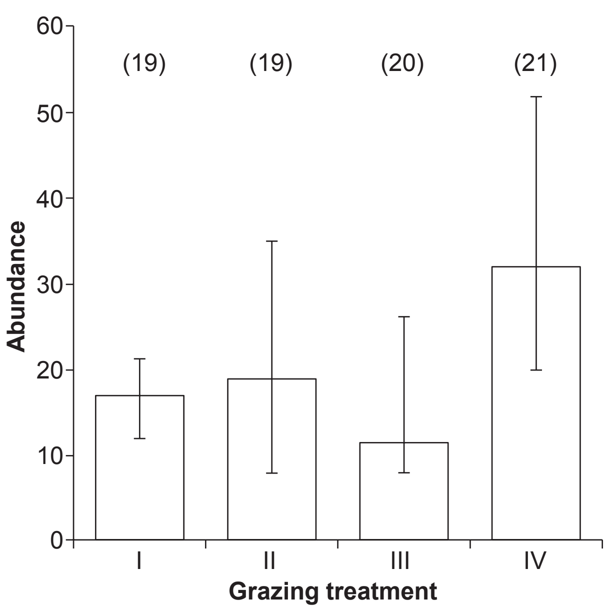

Fig. 3. Median and interquartile range of Auchenorrhyncha abundance in each grazing treatment from sweep net samples. Number of samples is shown in parentheses at the top of the chart. Grazing treatments as detailed in Fig. 1.

Grazing effect on assemblage in sweep net samples

Within the RDA of sweep net samples grazing treatment explained 17% of variation in the species assemblage data although this was marginally non-significant (F = 1.528,

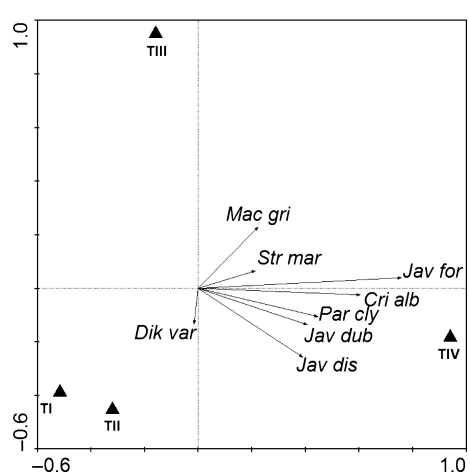

Fig. 5. Redundancy Analysis (RDA) ordination of D-vac samples showing grazing treatments as nominal environmental variable (▲ and labelled as TI to TIV) and species of which ≥10 individuals were recorded. Species codes: Cri alb, *Criomorphus albomarginatus*; Dik var, *Dikraneura variata*; Jav dis, *Javesella discolor*; Jav dub, *Javesella dubia*; Jav for, *Javesella forcipata*; Mac gri, *Macustus grisescens*; Par cly, *Paraliburnia clypealis*; Str mar, *Streptanus marginatus*.

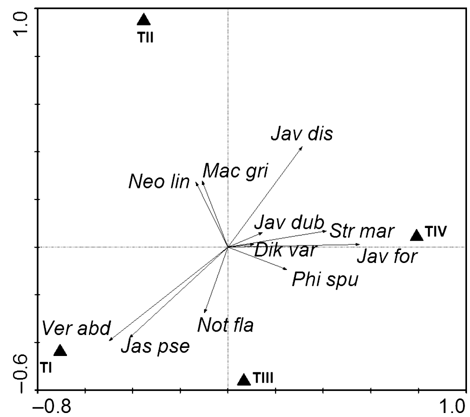

Fig. 6. Redundancy Analysis (RDA) ordination of sweep net samples showing grazing treatments as nominal environmental variable (▲ and labelled as TI to TIV) and species of which ≥10 individuals were recorded. Species codes: Dik var, *Dikraneura variata*; Jas pse, *Jassargus pseudocellaris*; Jav dis, *Javesella discolor*; Jav dub, *Javesella dubia*; Jav for, *Javesella forcipata*; Mac gri, *Macustus grisescens*; Neo lin, *Neophilaenus lineatus*; Not fla, *Notus flavipennis*; Phi spu, *Philaenus spumarius*; Str mar, *Streptanus marginatus*; Ver abd, *Verdanus abdominalis*.

P = 0.071). In this case, the high-intensity sheep grazing treatment (I) and the ungrazed treatment (IV) separated along axis 1 with the two low-intensity grazing treatments (II and III) separating more clearly on axis 2 (Fig. 6). The strongest species correlations with treatment in this biplot were of *Verdanus abdominalis* and *Jassargus pseudocellaris* which correlated strongly with the high-intensity sheep grazing treatment I.

Discussion

The highest number of Auchenorrhyncha were found in the ungrazed treatment and this follows expectation based on earlier work (e.g. Morris, 2000; Dennis *et al*., 2008). Grazing can suppress Auchenorrhyncha populations in a number of ways. At a basic level, livestock grazing reduces the quantity of plant biomass available to phytophagous insects (e.g. Bailey & Whitham, 2003) while some insect species suffer from grazing-induced reductions in structural heterogeneity (Dennis *et al*., 1998). The actions of grazing livestock can also affect insects physically, either though direct disturbance, such as being dislodged from foodplants (Kruess & Tscharntke, 2002), or through impacts of trampling (Morris, 2000). Furthermore, the more open vegetation created by grazing might facilitate greater movement of avian or invertebrate predators, further to the detriment of phytophagous species and indeed invertebrate predators have been shown to be more resistant to increases in grazing levels than have herbivores (Mysterud *et al*., 2010). Given these impacts of grazing, it is reasonable to expect an intermediate response of Auchenorrhyncha abundance in low-intensity (treatments II and III) compared to high-intensity (treatment I) grazing. Such a pattern has been reported by previous authors. For example, Kruess and Tscharntke (2002) reported decreasing numbers of Auchenorrhyncha along a gradient from long-term ungrazed pastures through short-term ungrazed pastures and extensively cattle-grazed pastures to intensively cattle-grazed pastures. Similarly Gibson *et al*. (1992), in an experiment on ex-arable land, found that abundance decreased with increased intensity and seasonal duration of sheep grazing. In our experiment, the high-intensity sheep grazing treatment I did marginally have the lowest abundance in D-vac samples, although in the sweep net samples abundance in treatment I was intermediate between (and not significantly different from) that in the low-intensity treatments II and III. Our results therefore give some limited evidence for an intermediate response in low-intensity grazing. Whilst a higher number of samples may have revealed a clearer result, the small magnitude of the difference between high- and low-intensity grazing compared to that for ungrazed plots indicates the particular importance of ungrazed areas for maintaining large Auchenorrhyncha populations.

Whilst the two sampling methods used here resulted in broadly similar patterns in abundance and species richness, the degree to which this pattern was evident differed to a large extent between them. Specifically, grazing treatments only showed a statistically significant difference when the D-vac was used as a collecting method. This reflects the fact that the two collection methods each sample different elements of the Auchenorrhyncha fauna. Sweep-netting is most efficient at collecting insects from the middle to upper layers of vegetation (hypergeic species) while D-vac sampling is more effective at sampling insects at or close to ground level (epigeic species) (Stewart, 2002). Our observations of greater abundance and species richness in the sweep net samples contrast with those of Standen (2000), who sampled in calcareous grassland, but are in keeping with the work of Moir *et al*. (2005). It is probable that the standing biomass of vegetation was higher at Glen Finglas that at Standen's site providing a proportionally greater resource for foliar species, and that this increased vegetation height had a negative effect on the efficiency of the suction sampling method, as demonstrated by Brook *et al*. (2008). In any case, Table 2 illustrates the complimentarity of the two approaches in covering the range of Auchenorrhyncha niches within the study site; only two of the 33 species were recorded by D-vac alone compared to 13 species recorded by sweep net alone but ten species were recorded more frequently in D-vac samples than sweep net samples.

Differences in the results from D-vac and sweep net samples can help shed light on processes acting on the Auchenorrhyncha community. The RDA biplot in Fig. 5 shows five species that are being strongly positively influenced by the ungrazed treatment IV (as listed in the results). All are graminoid-feeders, as indeed were the majority of species recorded (Nickel & Remane, 2002), and four of these five species were recorded most abundantly in D-vac samples (despite the lower overall total number for D-vac samples), suggesting that they are epigeic in nature. The habitat requirements of these species in Scotland are poorly known, though Nickel (2003) gives information on strategies adopted in Germany by all the species recorded in this study. Whilst traits shown in Germany might not necessarily correspond to those in Scotland they do give some indications that can, at least, assist with interpretation. To this end, all these spe-

Table 2. Auchenorrhyncha species recorded during sampling at Glen Finglas in 2007 together with total abundance from the two sampling methods used.

Taxon	Sweep net	D-vac
Fulgoromorpha		
Cixiidae		
Cixius nervosus (L., 1758)	1	0
Cixiidae sp. ♀	3	3
Delphacidae		
Delphacinus mesomelas (BOH., 1850)	0	1
Paraliburnia clypealis (J.SHLB., 1871)	3	53
Acanthodelphax denticauda (BOH., 1847)	3	3
Nothodelphax distincta (FL., 1861)	3	0
Dicranotropis divergens KBM., 1868	2	0
Florodelphax leptosoma (FL., 1861)	4	6
Xanthodelphax straminea (STÅL, 1858)	5	4
Paradelphacodes paludosa (FL., 1861)	1	8
Oncodelphax pullula (BOH., 1852)	2	4
Criomorphus albomarginatus CURT., 1833	7	13
Javesella discolor (BOH., 1847)	208	102
Javesella dubia (KBM., 1868)	64	94
Javesella forcipata (BOH., 1847)	272	420
Delphacidae sp. ♀	604	398
Cicadomorpha		
Aphrophoridae		
Neophilaenus lineatus (L., 1758)	299	2
Philaenus spumarius (L., 1758)	83	1
Cicadellidae		
Ulopa reticulata (F., 1794)	0	2
Oncopsis subangulata (J. SHLB., 1871)	1	0
Planaphrodes bifasciata (L., 1758)	4	0
Aphrodinae sp. ♀	1	0
Evacanthus interruptus (L., 1758)	2	0
Dikraneura variata HARDY, 1850	15	16
Forcipata citrinella (ZETT., 1828)	3	2
Notus flavipennis (ZETT., 1828)	26	2
Eupteryx notata CURT., 1937	1	0
Balclutha punctata (F., 1775)	4	0
Macrosteles sexnotatus (FALL., 1806)	5	0
Deltocephalus pulicaris (FALL., 1806)	5	0
Thamnotettix confinis (ZETT., 1828)	5	0
Macustus grisescens (ZETT., 1828)	68	53
Streptanus marginatus (KBM., 1858)	148	48
Jassargus pseudocellaris (FL., 1861)	114	4
Jassargus sursumflexus (THEN, 1902)	1	0
Verdanus abdominalis (F., 1803)	108	5

cies that are strongly associated with the ungrazed treatment IV are said to utilise shaded positions, this being consistent in grassland species with a dense grass *canopy* as epigeic species might encounter in particular within this treatment. Of two species closely positively correlated with the high-intensity sheep grazing treatment I in the RDA biplot of sweep net samples (Fig. 6), *V. abdominalis* is said to favour sunny sites whilst *J. pseudocellaris* has a preference for low-growing grass stands (Nickel, 2003). At Glen Finglas, the high-intensity sheep grazing in treatment I plots produced a lower mean vegetation height than in other treatments (in summer 2007 the mean heights in treatments I–IV respectively were 32.9, 41.5, 43.8 and 47.3 cm, R. Pakeman unpubl. data). Treatment I plots also contained some areas of very closely cropped ground and these are clearly exploited by the named species. On the other hand, *Macustus grisescens* and *Neophilaenus lineatus* are both species of tall vegetation but with a preference for a range of situations from sunny to moderately shady (Nickel, 2003), conditions that are apparently most prevalent in the low-intensity sheep grazing treatment II.

Different responses of presumed epigeic and hypergeic Auchenorrhyncha species to experimental treatments are rarely investigated, but epigeic species have been shown to exhibit a greater response to predator presence (Taraschewski *et al*., 2005; Sanders *et al*., 2008). Furthermore, a previous comparable grazing experiment replicated at the landscape scale failed to find a grazing treatment effect on Hemiptera (Mysterud *et al*., 2005). Sampling was carried out in that work by sweep-netting and was thus likely to have favoured the collection of hypergeic species and under-sampled those species that we found showing the greatest response to grazing treatments.

Ungrazed grasslands have the potential to harbour species that are largely absent from other grasslands. Furthermore, the development of the Auchenorrhyncha assemblage in undisturbed sites may be a gradual process. Although the data that we present here represent a snapshot from a single season, previous work on Hemiptera as a whole at the same study site as reported here suggests that there has been an increasing trend towards larger differences between ungrazed and grazed plots (Dennis *et al*., 2008) following the cessation of grazing in treatment IV. We know that colonisation of habitats by some upland Auchenorrhyncha species is dispersal-limited (Littlewood *et al*., 2009) and that newly created habitat may host an impoverished Auchenorrhyncha fauna (Nickel & Achtziger, 2005). These pieces of evidence together demonstrate that assemblages may take some years to respond to changes in management such as a reduction in grazing intensity. They additionally support the premise that long-term ungrazed areas may be important for harbouring significant populations of Auchenorrhyncha, with the work presented here suggesting that epigeic species in particular may benefit from such areas.

Upland land use in Scotland is seeing a trend towards lower numbers of livestock and, in some areas, complete abandonment of sheep and cattle grazing. Such extensification of land use may be to the benefit of a range of species. There is, however, likely to be a point at which grassland species are lost as scrub encroachment occurs. The limits at which this might happen are not well understood and it is important to take opportunities to consider invertebrate species turnover in habitat succession studies. Most replicated grazing experiments are relatively short-term, but land management decisions can have much longer-term impacts. As well as demonstrating varying responses of different Auchenorrhyncha guilds to grazing regimes, this study underlines the importance of long-term ecological experiments to help unravel complex interactions and associations.

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